The Intermuscular System of Acanthomorph Fishes: a Commentary

G. DAVID JOHNSON[1] AND COLIN PATTERSON[2]

We got some 'splainin' to do.
          Desi Arnaz, as Ricky Ricardo in "I Love Lucy"

You can't have your cake and eat it too.
          Ancient Proverb

ABSTRACT

This paper is a response to Gemballa and Britz (1998), who presented a new interpretation of the intermuscular bones of acanthomorphs, homologizing them with the epicentrals of lower teleosts. We argue that their identification of epineural ligaments above the intermuscular bones in many acanthomorphs is mistaken; the structures in question are fanlike arrays of collagen fibers, not true intermuscular ligaments. We show also that undisputed epineural intermusculars penetrate or enter the horizontal septum in lower acanthomorphs (*Velifer, Polymixia*, beryciforms), and reiterate arguments for regarding the single series of intermusculars in most acanthomorphs as epineurals, secondarily displaced into the horizontal septum.

[1] Curator, Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington DC 20560.
[2] Honorary Research Fellow, FRS, deceased 1998, Department of Palaeontology, The Natural History Museum, London.

INTRODUCTION

Gemballa and Britz (1998; hereafter referred to as "G & B") have published an account of the intermuscular bones and ligaments in acanthomorphs. Their interpretation of those structures differs in several ways from ours (Johnson and Patterson, 1993; Patterson and Johnson, 1995; hereafter referred to respectively as "J & P" and "P & J"). In brief, G & B's main conclusion is that the single series of intermuscular bones found in the vast majority of acanthomorphs are not epineurals displaced ventrally into the horizontal septum, as we proposed, but are epicentrals. [Incidentally, this was also the opinion of Richard Owen, who first named the three intermuscular series (1866), and believed that the bones in *Perca* and *Gadus*, the acanthomorphs in his sample, were epicentrals. As we wrote (P & J, p. 2), "we both initially thought Owen right."] G & B found that our conclusion resulted from inadequate technique, which led us to miss ligamentous elements of the intermuscular system in many of the acanthomorphs that we examined. The purpose of the present paper is to explain some of the differences between their observations and our own and the background to our conclusions; then to review the different interpretations of structure in some acanthomorph taxa; and finally to compare the two arguments for homology. In the Introduction to our paper (P & J) we wrote that our observations of ligaments "include an unknown quantity of subjectivity, and we will be glad to see all or any of them checked by others." We did not anticipate that we should so soon be required to check some of them ourselves. To anticipate our results, after a lot of work and some initial doubts, we are convinced that the intermuscular bones of acanthomorphs are epineurals.

TERMINOLOGY

Following advice from M. W. Westneat, G & B elected to use the name "tendon" for the connective tissue bundles in myosepta that we (P & J) named "ligaments." Their reasons for the change of name were: (1) the structures connect muscle to bone (axial skeleton); (2) the structures "transfer muscular forces from myomeres to the axial skeleton and thus act as tendons"; (3) when intermuscular bones develop within the structures, thereby justifying the term ligament for the proximal part joining bone to axial skeleton, the bone appears relatively late in ontogeny, "and we see no necessity to apply a different term to the same structure at a later point in ontogeny."

We regret and will oppose their decision to change the names, in part because the intermuscular system is already difficult, and to change the entire terminology only three years after the system was first mapped (in P & J) will not help communication. We also question the propriety of using tendon for all the structures that we called ligaments. The technical distinction is ambiguous in a number of cases. The term tendon was used for structures in the horizontal septum by Kishinouye (1923) and Kafuku (1950), who named the anterior and posterior oblique tendons (AOTs, POTs); Kafuku's AOTs are our epicentral ligaments (in lower teleosts) and epineural ligaments (in percomorphs). Kafuku named these structures tendons because they connect the lateralis superficialis (red muscle) with the axial skeleton. Westneat et al. (1993) gave a detailed account of the arrangement of AOTs and POTs in the horizontal septum of scombrids and their role in the transmission of forces to the axial skeleton. Among other things, they found that AOTs and POTs are joined distally into a loop by a segment of the POT that they called ITL (intertendon length)—"This loop is so robust that the fish can be lifted by it." Each POT slides relative to succeeding AOTs as it passes posteriorly, but a significant portion of its fibers converge with and join those of the distal end of the anteriormost AOT of the loop (Westneat et al., 1993: 195). Here then, AOT and POT together form what is technically a ligament, since it joins two bones (vertebrae). Also, although POTs generally insert in the lateralis superficialis, the anteriormost POTs may insert on intermuscular bones in percomorphs (P & J), here again meeting the technical criterion of ligament.

The other series of structures that we (P & J) named ligaments are the epineurals and epipleurals. Members of these series have been best illustrated by Gemballa (1995).

They attach to the axial skeleton proximally and lie in the myoseptum, where they fan out distally into an array of small fiber bundles that have no specific insertion in the body musculature. Some epaxial muscle fibers attach perpendicularly along the length of the intermusculars (be they ossified or unossified), as they do over the entire surface of the myoseptum, but the muscle fibers do not converge or concentrate at the points of insertion as is typically the case for tendons. G & B stated that such fibers "transfer muscular forces from myomeres to the axial skeleton and thus act as tendons" but this is to oversimplify, and of course the same then must be true of the entire myoseptum, as discussed by Van Leeuwen (1999). Furthermore, we are unable to reconcile G & B's conclusion (nor did they address it) about transmission of forces with the following statement from Gemballa (1995: iii), in which the term ligament was used for the unossified elements of all three series:

> Epineural and epipleural ligaments are unlikely to play a role in transmission of muscular forces because its collagen fibres and white muscle fibers include an obtuse angle. They resist the radial expansion of contracting muscle fibres of the VAC's and, DAC's and thus may stiffen the trunk during undulatory locomotion (bracing and bandaging "Querverspannungs-funktion"). Furthermore during sharp bendings these ligaments keep the relative positions of axial skeleton and integument to each other against the expanding musculature (holding device or guy, "Haltefunktion").

In a more recent paper, Gemballa (1998: 30) hypothesized that "Muscle arches consisting of white muscle fibers are reinforced by epineural tendons and lateral bands that **may** (emphasis ours) transmit forces to the backbone." It would appear that the precise function of unossified epineural and epipleural elements remains unresolved. Epineural and epipleural intermuscular bones, when present, are ossifications in the epineural and epipleural ligaments. G & B's statement, quoted above, means that the function of these intermuscular bones is to transmit the pull of muscles to the axial skeleton, but Wainwright (1983: 70) stated that "Intermuscular bones, when present, reinforce septa," and Van Leeuwen (1999), in his mechanical analysis of myomere shape, referred to the stabilizing effects of intermuscular

(which he called intramuscular) bones (specifically epineurals), and also used the term ligament for unossified intermuscular elements. Perhaps reinforcement and stabilization do not exclude a transmission of force function as well, but if the latter is the criterion by which we are to distinguish tendon from ligament, then structures such as the maxillo-mandibular ligament, semicircular ligament, and others must also be renamed.

G & B's usage also entails some ambiguity. For example, in describing *Velifer* they called the ligaments attaching the epineural bones of V7–10 "a short proximal tendinous sheath." We will therefore continue to use our earlier terminology, and call the connective tissue bundles ligaments, not tendons.

Abbreviations

BL Baudelot's ligament
cf collagen fiber
ecb epicentral bone (G & B only)
ecc epicentral cartilage
ecl epicentral ligament
enb epineural bone
ent epineural tendon (G & B only)
epb epipleural bone
lb lateral band (G & B only)
ns neural spine
V   vertebra

Institutional abbreviations are those of Leviton et al. (1985).

DIFFERENT METHODS; DIFFERENT CRITERIA; DIFFERENT RESULTS?

G & B used the following technique developed by Gemballa during work for his doctoral thesis (1995): cleared-and-stained (c & s) specimens are transferred from glycerin to ethanol; then individual myosepta are cut free, mounted on slides, and studied with polarized light. With this method, G & B are able to visualize the collagen fibers in a myoseptum far more accurately than we could, with our relatively primitive technique of observing c & s specimens under the stereomicroscope. Although we mentioned the value of transferring glycerin specimens to alcohol (P & J: 4), we made little use of the technique. This was in part because we felt that the procedure, like too much reliance on incident light, could cause us to record as

ligaments aggregations of collagen that did not deserve the name. We were anxious not to overinterpret the specimens. In our extensive survey of teleostean intermusculars (we recorded the system in about 125 genera) we had to develop a criterion for what should be called an intermuscular ligament and what should not. This is always necessary toward the caudal end of each series, where the ligaments become successively shorter and more subdivided distally, and is often necessary also at the cranial end of a series. Working in untrodden ground, we identified ligaments by trial and error, changing places at the microscope or passing specimens from hand to hand between two microscopes. We arrived at the following criterion of discreteness: we recorded as ligaments only those structures that, like ossified intermusculars, had a single origin on the axial skeleton, and were sufficiently discrete to be picked up distally by the forceps (recognizing that the latter criterion can have an element of subjectivity and is difficult to apply in the very smallest specimens). Where a series of bones is continued rostrally or caudally by ligaments our "discrete" structure characterizes those ligaments that lie immediately adjacent to the bones with which they are unquestionably serially homologous. With this criterion, we would not have recorded as ligaments many of the structures so labeled by G & B. This is true notably of their first epineural ligament (enl 1), which they label epineural tendon (ent) in *Polymixia* (their fig. 2B, our fig. 1A), and of the epineural ligament (tendon) in the following illustrations: their fig. 4B–D (ent 6, 3, 1 in *Hoplostethus*), fig. 6A (ent 15 in *Aphredoderus*), fig. 6B (in the midbody of *Molva*), fig. 6C (ent 15 in *Bedotia*), fig. 6D (in the midbody of *Scomberesox*), fig. 6E, F (ent 8, 2 in *Lates*), fig. 7A, B (ent 9, 3 in *Centropomus*), fig. 7C, E–F (ent 11, 2, 1 in *Morone*) fig. 8A–C (ent 15, 8, 2 in *Serranus,* fig. 8D, E (ent 8, 3 in *Pseudanthias*), and fig. 10E (ent 19 in *Channa*). We question also the epicentral ligaments (ecl) indicated in G & B's fig. 6E (ecl 8 in *Lates*) and fig. 7A (ecl 9 in *Centropomus*). We might argue about a few more of the illustrated structures, but we comment in detail below on those in the above list.

HISTORICAL ACCIDENT

As chronicled in the Introduction, our study of the intermuscular system began with an effort by one of us (CP) to understand the system in a large cleared-and-stained *Polymixia* where the epicentral series cannot be missed because the ligaments of V3–17 contain conspicuous cartilage rods. We agreed to collaborate after GDJ had seen a draft manuscript, found that intermuscular ligaments are far more widely distributed than CP had thought, and carried to London a number of c & s specimens. Notable among these were holocentrid and anomalopid beryciforms that seemed to show a continuous series of intermuscular bones and ligaments of which the first few members are in the horizontal septum (the usual position of epicentral bones and/or ligaments), the last few on the neural spines (the usual position of posterior epineurals), and the intervening members ascend successively further from the horizontal septum. Beneath some of those ascending bones, and beneath all of the posterior ones, is a series of epicentral ligaments, but that series seemed to us incomplete because none occurred on the first few vertebrae. *Polymixia,* on the other hand, has only the first intermuscular bone in the horizontal septum, those of succeeding vertebrae successively further above that septum, and an epicentral series of ligaments that extends forward to V2. These fishes, interpreted as a morphocline continued with further modification in percomorphs, were the key to our interpretation of acanthomorph intermuscular bones as descended epineurals. Later in our investigation of percomorphs, we found (inconveniently) that some of them had a series of ligaments above the intermuscular bones, in the position of the epineural series of lower teleosts. We had to interpret these as neomorphs, and called them neoneurals. We recorded them in representatives of almost 20 families (Ammodytidae, Bothidae, Caesionidae, Carangidae, Echeneidae, Gerreidae, Haemulidae, Kuhliidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Polynemidae, Pomacentridae, Samaridae, Scaridae, Sciaenidae, Sparidae, Teraponidae; they are ossified in the bothid and samarid pleuronectiforms we studied). Naturally, G & B took our

"neoneurals" to be the true epineural series, and used them to counter our argument of homology, based on interpretation of lower acanthomorphs.

However, as we extended our investigation into lower teleosts, we found a situation in aulopiforms that seemed to bolster, if not confirm, our argument that acanthomorph epineurals have descended into the horizontal septum, displacing the epicentrals. In aulopiforms the epineural series is normal, and there is no reason to question its homology with that of other lower teleosts. In the horizontal septum of almost all aulopiforms there is a series of bones that extends forward to V1 or V2. We first took these to be epicentrals, which ossify in a few other groups (e.g., *Megalops,* clupeomorphs, gonorynchiforms). But then we found aulopiforms in which the posterior "epicentrals" moved successively further below the horizontal septum until they occupied the ventral position normal for epipleurals, the third series of intermusculars. Some aulopiforms, notably a larva of *Scopelarchoides* (P & J: fig. 10) and the evermanellids (fig. 3), showed clearly that this ventral shift from the horizontal septum was accompanied by successively deeper distal subdivision, of ligaments (in larvae, P & J: fig. 10), or of bone with ligament attached dorsally (notosudids), or of bone ventrally and ligament (sometimes with included cartilage, ecc in fig. 3) dorsally. Here we had evidence of continuity between a series of bones in the horizontal septum anteriorly and well below it posteriorly, and in which identification as epipleurals seems incontrovertible, because the epicentral series can be identified as the ligaments inserting on the dorsal surface of the intermuscular bones in the zone of transition. With this evidence that it was possible for epipleurals to "migrate" dorsally into the horizontal septum, we were more comfortable with our interpretation of percomorph intermusculars as epineurals that had done the opposite trick, "migrating" ventrally into the horizontal septum. Holocentrids and anomalopids were our acanthomorph equivalent of aulopiforms like that in figure 3, demonstrating coexistence of the two series in the same segment.

REVIEW OF STRUCTURE

Here we review the intermusculars in some of the acanthomorphs described by G & B (we treat the taxa in the sequence that they used), and in a few other taxa recorded by P & J but not by G & B. We also comment on the POTs in these fishes, because they are relevant to our argument about homologies of acanthomorph intermusculars.

POLYMIXIIDAE

As noted above, our investigation began with *Polymixia,* and it was one of the keys to our interpretation of percomorph intermuscular bones as descended epineurals. It is also the key taxon in G & B's reinterpretation, which is based on Patterson's (1982) "conjunction test" of homology: homology between two structures (such as the wing of a bird and the arm of a mammal) is refuted if an organism (such as an angel) exhibits both. G & B argued that the intermuscular bone of V1 in *Polymixia,* which inserts in a socket at the base of the neural arch, is larger than its bony successors and (unlike them) lies in the horizontal septum, cannot be an epineural (and so must be an epicentral) because there is an epineural ligament above it in series with the epineural bones (and ligaments) of succeeding vertebrae. As also noted above, we would not have called their epineural 1 (fig. 1A; G & B, fig. 2B) a ligament: it is not a single, discrete structure, but an array of bundles of collagen fibers that have multiple origins on the neural spine and decrease in size dorsally and ventrally from the larger bundles in the center of the array. Furthermore, G & B's depiction (fig. 1B; G & B, fig. 2C) of the origin of that structure in the usual position of the first epineural, i.e., at the base of the neural arch near its attachment to the centrum, is inaccurate. Their illustration shows the collagen fibers attaching along an area from the dorsal margin of the proximal tip of the first intermuscular bone (their ecb) to a point above its insertion on the base of the neural arch below the dorsal margin of the centrum. As shown in their figure 2B (our 1A) and more clearly in our figures 2, 4, and 5, the lowest point of attachment of these collagen fibers is well above the insertion of the first intermuscular

bone (and the dorsal margin of the centrum) and they extend along the neural arch dorsally to near the base of the neural spine. These observations do not refute unequivocally the identity of this structure as an epineural, however G & B's interpretation of the first vertebra in *Polymixia* requires that the first epineural has been displaced dorsally from its primitive site of insertion (which often has a modified articular depression or even a well-developed socket, as in *Velifer*) and reduced from a robust bone to a diffuse array of collagen fibers, while the first epicentral has ossified and moved dorsally to occupy the usual insertion point of the epineural. More important, as shown in figures 2, 4, and 5, G & B's argument may be turned around, because on the neural spine of V2 there is an exactly similar, though slightly less extensive, array of collagen bundles. Beneath this is the intermuscular bone, which originates on the neural arch, lies above an epicentral ligament, and is inclined dorsolaterally like its successors. This must therefore be an epineural, yet above it is a "ligament" like that which G & B identify as epineural 1. We believe that this refutes G & B's conclusion that "there is strong and unambiguous evidence that the first vertebra of *Polymixia* has an epineural tendon [ligament]." Presence of a diffuse array of collagen bundles in the myoseptum above an undoubted epineural bone in myoseptum 2 of *Polymixia* also throws into question G & B's identification of similar arrays as epineural ligaments in other acanthomorphs (e.g., their figs. 7, 8).

Our argument (P & J: 33) that the first intermuscular bone of *Polymixia* is a descended epineural, not an epicentral, was supported in our view by the fact that in a 12 mm larva the bone is fully formed and develops in series with the epineurals (those of V2–6 are ossified), before the epicentral ligaments are recognizable. G & B "consider this argument as invalid because the identification of epicentral tendons [ligaments] in 12 mm long cleared-and-stained specimens seems impossible with their technique." Yet with that technique we had no trouble in observing a long series of epineural and epipleural ligaments in the specimen (P & J:

table 1), and we have since confirmed our observations.

We used Gemballa's technique of transfer of glycerin specimens to alcohol followed by dissection and polarization of individual myosepta to study and photograph the first two myosepta of *Polymixia* (fig. 2) and *Velifer* (fig. 6). Our technique differed only in that we used a stereomicroscope, so that our photographs are of intact epaxial myosepta, whereas G & B used a compound microscope, and reassembled several photographs to cover the entire myoseptum. We agree that Gemballa's technique provides a superb way to visualize collagen fiber in myosepta, however our figures 4 and 5 of two intact c & s *Polymixia* in ethanol show that removal and polarization of individual myosepta are not essential for accurate observation of intermuscular ligaments or the arrays of collagen fibers (cf) identified as such by G & B. It does, however, prove informative in an unexpected way. Note that in figure 2 of the polarized myoseptum 2 in *Polymixia,* bone (enb) and true ligament (BL and ecl) are essentially indistinguishable and look nothing like the arrays of collagen fiber (cf) above each bone.

Notice also in figure 2B that the epicentral ligament originates not on the vertebra but on the base of the epineural; we had not observed this in intact c & s specimens, but have checked it by removing myoseptum 2 from the large *Polymixia* illustrated in P & J's figures 1 and 2. This means that the proximal end of epineural 2 must penetrate the horizontal septum (which contains the epicentral), and is evidence that epineurals may enter that septum.

In *Polymixia* (P & J: fig. 3) we found the first POT to originate on V8 and insert on the epicentral ligament of V5.

LAMPRIDIFORMES

VELIFERIDAE: We no longer have access to the specimens of *Metavelifer* and *Velifer* that we recorded (Patterson and Johnson, 1995: table 7). G & B do not differ from us in their interpretation of the intermuscular bones as epineurals. The only difference between their observations and ours concerns the epicentral ligament of V1: G & B failed to find one.

We recall our own doubts about that structure. (Our specimen had been much dissected before the drawing in J & P, fig. 1C, was made.)

We have removed myosepta 1 and 2 from a new specimen of *Velifer* (fig. 6). Epicentral ligament 1 is slender and (on both sides of the specimen) originates on the epineural bone rather than on the centrum. As with the origin of epicentral 2 in *Polymixia* (above), this means that the proximal part of epineural 1 enters the horizontal septum. Above the epineural in myosepta 1 and 2 there is an array of collagen fibers corresponding to those in myoseptum 1 and 2 in *Polymixia*, but inserting distally on the epineural. Our picture of myoseptum 1 in *Velifer* (fig. 6A) is very different from that in G & B (fig. 3D), and we have confirmed our observations on the other side of this specimen and both sides of an additional specimen from the same lot. The portion of the septum that in our specimen contains the epicentral ligament is filled with a tangle of fibers in their specimen, and above the epineural, their specimen contains an array of collagen fibers that does not insert on the epineural, and so is more like the corresponding array in *Polymixia*. The other obvious difference is merely an artifact resulting from G & B having cut away most of Baudelot's ligament, the remnant of which is visible as a dark structure at the anteroventral corner of the myoseptum. We also note here that the first epineural inserts in a socket at the base of the neural arch of V1 that is essentially identical to that in which the first intermuscular bone of *Polymixia* inserts.

In myoseptum 2 of *Velifer* (fig. 6B) the epicentral ligament is slender and originates on the centrum. Above the epineural an array of collagen fibers inserts on the epineural distally, as in myoseptum 1. G & B's illustration of myoseptum 4 in *Velifer* (G & B, fig. 3C) shows an array of fibers above the epineural similar to that in myoseptum 1 of their specimen, but its origin is a bit more concentrated and it is more extensive, converging on the epineural bone distally and extending beyond it.

G & B did not comment on the POTs (posterior oblique ligaments) of veliferids. In *Velifer* we (P & J: 40) recorded the first (most anterior) POT as originating on V9 and inserting on the epicentral ligament of V3. G & B's (fig. 3) illustrations of *Velifer* show POTs on the epicentral ligament of V11, but none are recognizable in their photographs of myosepta 9 and 4.

LAMPRIDIDAE: G & B found that the first two intermuscular bones of *Lampris* originate on the centrum rather than the neural arch, where we placed them. Our observations were based on two large dried skeletons, USNM 271011 and 273477. The first neural arch is fused to the centrum in *Lampris*, and has an unusual configuration because the exoccipital portions of the occipital condyle extend dorsally to enclose the foramen magnum (Olney et al., 1993: 157). Our belief that the facet or groove for the intermuscular is on the neural arch is confirmed by the 19 mm larva figured by Olney et al. (1993: fig. 7), in which the first epineural originates on the neural arch. On V2, where the neural arch is also fused to the centrum, the point of origin of the intermuscular is debatable; the bone is not yet ossified in Olney et al.'s larva, and in our dried skeletons it might be taken to originate either on the base of the neural arch or on the centrum.

BERYCIFORMES

HOLOCENTRIDAE: In their specimen of *Holocentrus rufus*, G & B (their fig. 5) found "some peculiar changes of the intermuscular bones in myosepta 6 to 1, which we did not observe in other teleosts." Like us (P & J, p. 34, *Holocentrus* (*Sargocentron*) *diadema*; table 7, *H.* (*S.*) *spinifer, H.* (*Adioryx*) *vexillarius*) they found that the intermuscular bones of Vl and V2 lie in the horizontal septum. (We placed the origin of both on the neural arch whereas they placed the origin of that of V2 on the centrum; cf. Rosen, 1985: fig. 20; P & J: fig. 13.) They interpreted both these bones as epicentrals. In the myosepta of V3–5 G & B found intermuscular bones that "undergo a remarkable ventral shift" (p. 22). According to G & B, they are unattached proximally, and "are in a position neither epineural nor epicentral but somewhat intermediate. There is still an epicentral tendon [ligament] beneath these bones. The strong epineural tendon [ligament] of the

midbody myosepta is not present here" (p. 12). Instead of the epineural ligament, above these bones in myosepta 3–5 G & B illustrated a fanlike array of collagen bundles, whose origin on the neural arch or spine is marked with an arrow in G & B's figure 5. In myoseptum 6 (G & B: fig. 5D) this fanlike array is also present above the intermuscular bone (marked with an asterisk), which originates on the rib and which G & B acknowledged is an epineural, like the bones and ligaments on succeeding vertebrae. The fanlike array is more extensive in myoseptum 6 than in 5 (G & B: fig. 5E), whereas in myoseptum 4 (G & B: fig. 4F) the fibers are shorter but more concentrated than in 5. The array becomes a diffuse mass in myosepta 1 and 2 (G & B: fig. 5G, H). G & B (p. 22) wrote of these arrays "It is not clear whether an epineural tendon [ligament] is present as well." They were also "not sure how to interpret" the bones lying between the epineural and epicentral position [on V3–5]. Because we have not seen a similar arrangement in any other species, we are inclined to interpret these as autapomorphic for Holocentridae. Our own interpretation of those bones is that they are unquestionable epineurals, because beneath some of them (as G & B have shown) there are epicentral ligaments, and because in other holocentrids they attach to the axial skeleton (to the rib; below). The arrays of collagen fibers above the bones therefore cannot be epineural ligaments, and, like the similar arrays above epineural bones in *Polymixia* and *Velifer* (above), they are further evidence that similar arrays in other acanthomorphs are not necessarily epineurals.

Our observations of holocentrids (P & J, p. 34, principally *H. (Sargocentron) diadema*) differed from those of G & B in that we found no epicentral ligaments anterior to V9, whereas in *H. rufus* they illustrated such ligaments (their fig. 5) on V4–8 and reported one on V3. We also found that the first POT originates on V13 and inserts on the integument together with the epicentral ligament of V9 (the first that we observed). G & B seemed to confirm this, since in their illustrations the only POT shown lies about halfway along the epicentral ligament of V10. Like G & B, we found that the intermuscular

bones of V6 and 7 originate on the rib; unlike them, we found the bones of V3–5 also attaching directly to the rib (rather than floating free, as in their *H. rufus*). If these bones attach to the rib, at least their proximal part must lie in or penetrate the horizontal septum, which has to be dorsal to the ribs. Here, then, we have unambiguous evidence that an epineural bone (G & B acknowledged that at least those of V6 and 7 are epineurals) may migrate ventrally and enter the horizontal septum. We (P & J: tables 1–5) found no lower teleost in which epineurals entered the horizontal septum, although we found several examples (P & J: p. 12) of epineural origin shifted ventrally to the centrum, and even to the parapophysis (in the aulopiform *Scopelosaurus*). In holocentrids, our interpretation of continuity between the intermusculars of V1 and 2 (in the horizontal septum, the epicentral position) and those of succeeding vertebrae (successively further above that position) is corroborated, in our view, by the occurrence of superficial plates of cartilage surrounding the tips of the first three bones in our *H. diadema* (P & J: fig. 13) and the first four in *H. spinifer* (P & J: table 7). These superficial cartilages may occur at the tips of the first five bones (USNM 304760, three c & s *H. (Sargocentron)* sp., Aldabra).

We have rechecked our observations of holocentrids in c & s *Holocentrus ascensionis* (USNM 336175, SL 84 mm) and *Plectrypops lima* (USNM 288860, SL 61 mm), both transferred from glycerin to alcohol. In *H. ascensionis,* as with the other holocentrids that we recorded (P & J: p. 34 and table 7), we found the first recognizable epicentral ligament originating on the parapophysis of V9. It is smaller than that of V10, and consists of two separate, parallel strands, the lower slightly larger than the upper. In the next four myosepta (of V5–8), where G & B (figs. 5B–E) illustrated epicentral ligaments, we see nothing worth calling a ligament, although in some of these septa there are much less conspicuous double bands of connective tissue like that on V9. We infer that these double bands border the junction between the horizontal septum and the myoseptum, where there will inevitably be some concentration of connective tissue. In myoseptum 4 there is a more recognizable epicentral ligament.

As in G & B's illustration of that septum (fig. 5F) the ligament runs just below and parallel to the intermuscular bone; distally it converges on the bone and attaches to its tip. In myoseptum 3 we see no trace of a ligament. Nevertheless, if G & B are correct in recording epicentral ligaments forward to myoseptum 3 in *Holocentrus,* those ligaments have no bearing on general questions of homology except to reinforce interpretation of the intermuscular bones in myosepta 3–5 as epineurals. In their *H. rufus,* G & B found these bones to be unattached proximally. In our *H. ascensionis* the intermuscular bone of V3 is attached directly to the rib, but those of V4 and 5 are unattached. A very strong sheet of connective tissue originates medial to these two bones, on the heads of the second and third ribs (on V4 and 5). It is composed of numerous parallel bands of collagen that run anterolaterally and insert mainly on the intermuscular bone of V2, and partially on that of V1. As in our other holocentrids, the first POT in *H. ascensionis* originates on the hemal spine of V13 and inserts at the tip of the epicentral ligament of V9, the first conspicuous one.

In *Plectrypops lima* there are 12 or 13 intermuscular bones. The first two originate on the neural arch. The first is slender; the second is much stouter, with a proximal knob fitting a socket at the base of the neural arch. Intermusculars 3–8 originate on the rib, 3–4 and 7–8 near the head of the rib, 5–6 further down the shaft. These intermusculars, 6–7 in particular, remain close to the rib for the proximal part of their course, and the tips of 1–7 are all on or very close to the lateral line nerve. Intermusculars 9–11 originate successively higher on the hemal spine, 12 on the centrum, and 13 (which is diminutive) on the neural arch. The tips of intermusculars 8–12 end successively further above the lateral line nerve. In the epicentral series, we find recognizable ligaments forward to V5, where the ligament originates on the rib, distal to the origin of the intermuscular bone. The epicentral ligaments of V5–7 run out close below the bone, and converge with it distally to attach to its tip (as with the ligament of V4 in *H. ascensionis,* above). Beyond V7, bone and ligament diverge distally, successively more in each myoseptum. G & B illustrated what appears to be the same pattern in *H. rufus* in their figure 5E (myoseptum 5), where bone and ligament converge and meet distally; in their fig. 5D and F (myosepta 6 and 4) bone and ligament converge distally, and their tips may be cut off.

G & B supported their belief that the intermuscular bones in myosepta 3–8 are not in series with the bones of V1 and 2 (in the horizontal septum) by observation of holocentrid larvae in which the bones of V1 and 2 are ossified at 11 mm, whereas those of V3–6 do not ossify before 26 mm. This difference (confirmed by our observations of holocentrid larvae) may be explained by differentiation of the bone on V2. It is the main site of insertion of the strong sheet of connective tissue described above, is larger than its neighbors, and has an enlarged head (P & J: fig. 13; Rosen, 1985: fig. 20, *H. rufus*). In any case, delay between ossification of the intermusculars of Vl–2 and those of succeeding vertebrae is not evidence that they belong to different series. Potthoff and Tellock's (1993) account of development in *Centropomus undecimalis* shows that the intermusculars of Vl–2 ossify at 7–8 mm, whereas those of succeeding vertebrae do not appear until about 13 mm, when the animal has almost doubled in length. In *Centropomus* there is no question about serial homology of the intermusculars.

ANOMALOPIDAE: G & B did not study anomalopids. In *Anomalops* (P & J: table 7) we recorded a situation much like that in holocentrids, with intermuscular bones originating on the neural arch and lying in the horizontal septum on V1 and 2, originating on the rib on V3 and 4, on the parapophysis on V5–10, the centrum on V11, and thereafter a series of epineural ligaments ascending from the centrum to the neural arch in successive segments. We found the bones of V3–6 to be partially in the horizontal septum. Our first epicentral ligament was on V11, beneath the last ossified intermuscular. We found the first POT originating also on V11, and wrote (P & J: p. 40) "Because there are no epicentrals anterior to this, POTs of V11–13 lie free in the horizontal septum as they pass forward after crossing the epicentral of V11." Checking this and two other c & s specimens after transfer to alcohol, we

found discrete epicentral ligaments extending forward to V9 and, additionally, one attaching to the epineural bone of V1 and sometimes V2. More diffuse collagen arrays attach to the ribs of V3–V8. In one specimen the last epineural bone is on the neural arch of V14. Posteroventrally directed fiber arrays (similar to those identified as epineurals by G & B in *Hoplostethus,* see below) are detectable from V1 to V8–9, the posteriormost the weakest. Dissection of a whole alcoholic specimen revealed the first seven intermusculars partially in the horizontal septum.

In *Photoblepharon* (P & J: table 7) we recorded a pattern different from that in *Anomalops,* with a gap in the epineural series between the two bones originating on the neural arch on V1 and 2 and a ligament on the rib of V6. Thereafter we recorded an epineural ligament on the rib of V7, ligaments with included bone on the parapophyses of V8–12, and ligaments on the neural arch or spine beyond that. We placed the ligaments of V6–8 partially in the horizontal septum. Our first epicentral ligament was on the parapophysis of V10. Checking these observations in two larger (69 and 80 mm) c & s specimens of *Photoblepharon* that were transferred from glycerin to alcohol, we found that the first ligament originates on the rib of V4, and that it and the succeeding ones are entirely in the horizontal septum and so in the epicentral position. They are relatively broad and could be epineurals, epicentrals, or a coalescence of the two, because on V8 and V9 epicentral ligaments and epineural bones (or ligaments with included bone) share the same origin, at the junction of rib and parapophysis, and diverge distally. Beyond that, epineural ligaments (with included bone distally to V12) gradually ascend the centra, the last inserting on the base of the neural arch of V15–17, while the epicentral ligaments continue posteriorly on the parapophyses. As in *Anomalops,* there are fiber arrays anteriorly (similar to those identified as epineurals by G & B in *Hoplostethus,* see below), the last and weakest one above the epineural bone of V8. The first POT in *Photoblepharon* originates on V14 and inserts at the tip of the ligament of V9.

BERYCIDAE: G & B did not study berycids. In *Centroberyx affinis* (P & J: table 7; our

specimen is a poor one) we again found a situation like that in holocentrids: bones on the neural arch and in the horizontal septum on V1 and 2, partially in the horizontal septum on V3–6, where they originate on the rib (3–5) or parapophysis (6), and ascending thereafter to the centrum and eventually (as ligaments) to the neural arch. We found the first epicentral ligament on V9. The epineural arrangement is much the same in a specimen of *Beryx splendens* (USNM 306134, SL 116 mm), where the epicentral ligaments extend forward to at least V8.

TRACHICHTHYIDAE: We have checked our observations of *Hoplostethus* (P & J: table 7) in three new (and much better) c & s specimens of *H. mediterraneus* transferred to alcohol. On the bases of the hemal arches of V8–13 there are conspicuous ligaments that we recorded (on V9–13) as epicentrals. We were wrong. G & B correctly interpreted these as epineurals, and believe that they, together with the horizontal septum and its included epicentrals, underwent "a ventral shift" in the middle part of the body, from about V6–15. We (P & J: table 7) recorded intermuscular bones (our epineurals) on Vl and 2 in *Hoplostethus,* but found no epineural ligaments beyond them. G & B (fig. 4) illustrated what they called epineural ligaments in myosepta 6, 3, and 1; these are diffuse arrays of collagen bundles, similar to those they illustrated on V1 in *Polymixia* (compare their figs. 2 and 4D, of myoseptum 1 in *Polymixia* and *Hoplostethus*) and on V1 and 4 in *Velifer* (compare their figs. 3C and 4C, of myoseptum 4 in *Velifer* and 3 in *Hoplostethus*). On V5–7 in *Hoplostethus* these arrays originate broadly low on the neural arch, whereas in more anterior vertebrae their line of attachment ascends the arch, until on V1 it is at the base of the neural spine (in G & B's fig. 4D, of myoseptum 1; notice the distance between it and the intermuscular bone, inserting on the neural arch). Therefore, these arrays reverse the normal pattern for epineurals, which always move from the neural arch anteriorly to the neural spine posteriorly. Further, the fibers are directed posteroventrally, rather than posterodorsally, the normal orientation of epineurals. In two of our specimens (USNM 307556, SL 73 mm; USNM 307273, SL 75 mm) the array of fi-

bers on the neural arch of V7 is smaller than that on V6, and on the neural arch of V8 (the first with an obvious epineural ligament on the base of the hemal arch) there is an even smaller array, (It is just visible in G & B's fig. 4A, of myoseptum 8, where it originates below, and then crosses, the guideline from the label ''ent.''), with no similar array on V9. In the third specimen (USNM 306625, SL 90 mm), however, it is well-developed on V9, where it becomes more condensed distally and joins the epineural ligament below it. Coexistence of the true epineural ligament and at least a remnant of the dorsal array of fibers in the same segments (V8 or V8–9) shows that the latter cannot be an epineural ligament, and we believe that there are no epineural ligaments anterior to V8. In a smaller *H. mediterraneus* (VIMS 4900, SL 41 mm), G & B's fiber arrays become increasingly difficult to detect from V1 posteriorly, whereas the epineural ligaments on V8–13 are fully formed, discrete structures like those in larger specimens, again casting doubt on homology of the two series.

G & B recorded epicentral ligaments forward to V3 in *Hoplostethus,* and found them to be in series with the intermuscular bones on V1 and 2 (their epicentral bones, our epineurals). We (P & J) missed the epicentral ligaments because we mistook epineurals for them. We now agree with G & B that they extend forward to V3. That of V3 originates well down on the rib (not on the centrum, where G & B place it), as do those of V4–6. That of V7 originates higher on the rib, and that of V8 at the tip of the hemal spine, below the first epineural ligament. Thus the ''ventral shift'' of the epicentral series that G & B believed took place ''toward the midbody'' in fact takes place much further forward, because the horizontal septum is confluent with the peritoneum anteriorly and is applied to the first rib (on V3) for its proximal one-third, down to the point of origin of the epicentral ligament. Consequently a ''ventral shift'' of the horizontal septum at midbody would not explain the abrupt ''shift'' in epineural origin that would help to homologize their ''epineural ligaments'' on V1–7 with the epineural ligaments of V8–13.

SUMMARY OF BERYCIFORMS

Holocentrids, *Anomalops,* and berycids have an unquestionable series of epineural bones from V3 onward, an interpretation now further confirmed by G & B's (and our own) observations of epicentral ligaments beneath anterior members of the series in holocentrids. In all three taxa, the anterior members of the epineural series originate on ribs (V3–4 in *Anomalops,* V3–5 in *Centroberyx* and *Beryx,* and V3–7 or V8 in holocentrids; in *Holocentrus* the bones are unattached proximally on V3–5 in G & B's *H. rufus* and on V4–5 in our *H. ascensionis*). Because they originate on ribs, these bones must enter the horizontal septum, which always lies dorsal to the ribs, and the attachment of epicentral ligaments to the distal ends of some of the bones in holocentrids shows that their tips are also in the horizontal septum.

In the anomalopid *Photoblepharon,* there is a series of discrete ligaments in the epicentral position attaching to the ribs of V4–7, beyond which the epicentral and epineural series are distinct, although the epicentral ligaments and epineural bones share a common origin on the ribs of V8–9. Do the ligaments on V4–7 belong to the epicentral or epineural series or represent both? The absence of included bone implies that they are epicentrals, but no conclusive answer is possible.

In the trachichthyid *Hoplostethus,* the first undoubted epineural is on V8, a ligament attached to the hemal arch. The epicentral series extends forward to V3, as ligaments attached to the rib or (V9) hemal arch.

OTHER LOWER ACANTHOMORPHS

We (P & J) found no epineural ligaments in paracanthopterygians, stephanoberyciforms, zeiforms, and lower percomorphs. G & B did not study stephanoberyciforms or zeiforms. In the paracanthopterygians *Aphredoderus* and *Molva,* the atherinomorphs *Bedotia* and *Scomberesox,* and the percoids *Lates, Centropomus, Morone, Serranus,* and *Anthias* they illustrated (figs. 6–8) what they call epineural tendons [ligaments] in myosepta from the midbody region in the two paracanthopts and two atherinomorphs, and from a range of myosepta in the percoids.

Without exception, these are diffuse arrays of fibers, like those that they illustrated on V1 in *Polymixia,* on V1 and 4 in *Velifer,* on V1, 3, and 6 in *Hoplostethus,* and on V4–6 in *Holocentrus* (their figs. 2B, 3C–D, 4B–D, 5D–F). The arrays in those lower acanthomorphs are discussed above and shown not to be epineurals. G & B seem to have their own doubts about some of these arrays in percomorphs, calling that in *Bedotia* "inconspicuous" and that in *Scomberesox* "a faint structure consisting only of a few strands".

In G & B's series of illustrations of percomorph myosepta, it is not until figures 9–10 that we find structures comparable with a true or indisputable epineural ligament (e.g., their figs. 2A, 3A, 4A, myoseptum 13 in *Polymixia,* 11 in *Velifer,* 8 in *Hoplostethus*). Those illustrations (their figs. 9–10) are of *Kuhlia,* two carangids, and *Sphyraena.* We reported our "neoneurals" in *Kuhlia* and some carangids (P & J: 41), but not in our 46 mm specimen of *Caranx chrysos* (P & J: table 8), or in *Sphyraena,* where we studied a 14 mm larva and a 79 mm subadult. Rechecking a larger specimen of *Caranx chrysos* (USNM 167629, SL 93 mm), we found 11 neoneurals. The fourth and fifth insert well up on the anterodorsal margins of the neural arches of V5 and V6, respectively, the sixth inserts higher on the neural arch of V7, and the remaining five insert successively higher on the neural spines of V8–12. The insertion pattern of the anterior three neoneurals is unusual and unlike any we have seen for true epineurals. The first two insert on the ligamentous tissue between the neural arches of V1 and V2 with some fibers attaching to the posterior margins of each arch, and the third inserts only on the ligamentous tissue between the neural arches of V2 and V3, having no direct attachment to either.

Rechecking another c & s *Sphyraena sphyraena* (USNM 272103, SL 83 mm) after transfer to alcohol, we found small ligaments originating on the head of the rib of V3–4, on the anteroventral corner of the centrum of V5–8, ascending to the middle of the front edge of the centrum by V10, and to the prezygapophysis by V14, which has the last ligament we could see. We would have to interpret these as neoneurals; the ligaments originate lower on the axial skeleton than

neoneurals in other percomorphs (P & J: table 8), where they usually attach relatively high on the neural arch (often well above the centrum) or on the neural spine, the usual position of the more diffuse collagen fibers that G & B homologized with epineurals.

There is considerable variability in neoneural patterns, but the most common appears to be one in which the first recognizable neoneural is on V2–3 relatively high on the neural arch, the next several descend a bit lower on the arch and then gradually ascend onto the neural spines. We have observed this pattern in the following: the gerreid *Eucinostomus* sp. (USNM 297254), the sciaenid *Leiostomus xanthurus* (USNM 323749), the haemulid *Microlepidotus inornatus* (USNM 292781), the mullids *Mulloidichthys samoensis* (USNM 272965) and *Upeneus tragula* (BMNH uncat.), and the pomacentrid *Dascyllus aruanus* (BMNH uncat.). In the polynemids *Polydactylus virginicus* (BMNH 67.8.16.312) and *P. sextarius* (USNM 297257) there is a well-developed neoneural high on the neural arch of V1; the succeeding neoneurals descend onto the centra and then gradually climb up onto the neural spines. In the ammodytids *Ammodytes dubius* (USNM 302241) and *A. tobianus* (BMNH uncat.), the first neoneural occurs on the parapophysis of V5, and a long series continues posteriorly on the centra, eventually climbing up the neural arches onto the neural spines.

As for the epicentral series in the (nonberyciform) lower acanthomorphs studied by G & B, they interpreted all the intermuscular bones as epicentrals, and reported continuity between those bones and a series of epicentral ligaments in *Aphredoderus, Lates, Centropomus,* and *Morone,* fishes in which we found either no epicentrals (*Aphredoderus*), or (in the three percoids) a gap between the bones and ligaments on anterior vertebrae (our epineurals) and the epicentral ligaments on caudal vertebrae.

Rechecking *Aphredoderus* in a better c & s specimen transferred to alcohol (USNM uncat., SL 43 mm), we found bones on V1–5 followed by small ligaments on V6–8 (P & J had 8 bones, G & B have 9), then a gap until V13, where the first epicentral ligament occurs. P & J (p. 40) failed to find POTs in

any paracanthopterygian, but G & B (fig. 6A) illustrated a POT in myoseptum 15 of *Aphredoderus.* We now agree, based on our alcoholic specimen, that slender POTs are present; the most anterior that we could detect originates on the parapophysis of V12 (last abdominal), and inserts on the integument with myoseptum 9.

In *Lates,* we checked another individual from the lot of BMNH planktonic young (*L. lonigispinus* or *niloticus*) recorded in P & J (p. 35, fig. 14), using alcohol and polarized light. Previously we recorded a gap of four vertebrae between the last intermuscular bone, on V5, and the first epicentral ligament, on V10. This second individual has a gap of three vertebrae, with the first epicentral on V9. G & B reported that in *Lates calcarifer* the epicentrals are "hard to recognize" on V4–9, and illustrated myoseptum 8 (fig. 6E). We find our assertion that there are no epicentrals on these vertebrae confirmed by G & B's photograph, in which the epicentral guideline points to nothing. In this specimen the first POT runs from V6 to the intermuscular bone of V3, not from V7 to the intermuscular of V4 as it did in P & J's specimen (p. 35). We also checked a larger *L. niloticus* (USNM 166851, SL 72 mm) in alcohol, and found a gap of four vertebrae between the last of the anterior series of bones (Vl–5) and ligaments (V6, perhaps V7) and the epicentral ligaments (Vl2 onward).

In *Centropomus* (*C. parallelus,* USNM 306578, SL 66 mm, checked, bones on V1–7) and *Morone* (*M. americana,* USNM 109851, bones on V1–7) the gap is smaller, only 2–3. G & B referred to the epicentrals of *Centropomus* as "weakly developed" on vertebrae immediately behind those bearing intermuscular bones (on V1–8 in their *C. robalito*). They illustrated myoseptum 9 (fig. 7A), and in our opinion the epicentral guideline leads to nothing recognizable as a ligament.

TWO ARGUMENTS FOR HOMOLOGY

G & B summarized their argument as three statements:

(1) the intermuscular bone on V1 of *Polymixia* is not an epineural,

(2) other beryciforms like *Hoplostethus* have epineural tendons [ligaments] dorsal to their series of intermuscular bones, and

(3) centropomids also possess a series of epineural tendons dorsal to their series of intermuscular bones.

For these reasons we conclude that Patterson and Johnson (1995) were misled in homologizing the single series of intermuscular bones with epineurals of lower teleosts.

(1) We have shown that G & B's case for an epineural ligament on V1 in *Polymixia* fails, because there is a similar "ligament" on V2 above an undoubted epineural bone (figs. 2–4, 5), and because G & B illustrated comparable arrays of fibers on V1 and V4 of *Velifer,* again above undoubted epineural bones.

(2) We have shown also that G & B's case for epineural ligaments above the intermuscular bones in beryciforms fails. In *Hoplostethus* their "tendons" do not exhibit the structure or relationships of epineural ligaments, and the series extends to V8 or V9, where it coexists with an undoubted epineural. In *Holocentrus* the similar "ligaments" (see arrows in G & B's fig. 5D–F) on V4–6 lie above bones that must be epineurals because there is an epicentral ligament beneath some of them.

(3) In centropomids G & B's identification of epineural ligaments is not refutable (as are points 1 and 2) by the conjunction test of homology, because there is no other undisputed trace of the epineural system in those fishes. We find that G & B's "epineurals" in centropomids (and other lower percoids, their figs. 6E–F, 7, 8) and their misidentified "epineurals" in *Polymixia* and beryciforms show enough resemblance to prove that their identification is wrong. For those unconvinced, we offer the following, less direct, phylogenetic arguments.

Veliferid lampridiforms are the only acanthomorphs with an unmodified intermuscular system, comparable with that in outgroups. In particular, they have a complete epineural series, from V1 onward (G & B agree). This is one of four characters that led us (J & P) to place lampridiforms as the sister group of all other acanthomorphs, distinguishing *Polymixia* plus higher acanthomorphs (Euacanthomorpha) by "First epineural displaced ventrally into the horizontal septum" (J & P: character 8, p. 601), but this epineural main-

taining its insertion in a well-defined socket at the base of the neural arch like that into which the first epineural of *Velifer* inserts. G & B found this character invalid, and asserted that "the phylogenetic position of Lampridiformes basal to Polymixiiformes needs critical reexamination." But G & B determined that veliferids are the only acanthomorphs with an epineural on V1, and therefore G & B differ from us only in interpreting the bone on V1 in *Polymixia* as an epicentral. With G & B's interpretation, our euacanthomorph character remains valid but must be rewritten as follows: *First epineural reduced from a conspicuous bone to a diffuse array of collagen fibers, with its origin displaced dorsally, from distinct socket at base of neural arch to a broad area along the arch extending from a point above the dorsal margin of the centrum to near the base of the neural spine; first epicentral ossified and with its origin displaced dorsally from centrum to distinct socket at base of neural arch.*

Because *Polymixia* differs from veliferids in having the epineurals of V3–10 originate on the parapophysis (V3–8) or centrum (V9–10) rather than on the neural arch, we also characterized Euacanthomorpha by "Point of origin of anterior epineurals displaced ventrally on to centra or parapophyses" (J & P: character 11, p. 602). We have now also found (fig. 2B) that the proximal end of the second epineural enters the horizontal septum in *Polymixia* (because the epicentral originates from it). In G & B's interpretation, all this would merely be autapomorphic for *Polymixia*. We thought it more significant, because the ventral displacement aligns the origin of the anterior epineurals with the intermuscular of V1. We found the same origin of the anterior intermusculars (on centra or parapophyses) in stephanoberyciforms, but there the bones are all in the horizontal septum and there are no epineurals above them. In G & B's interpretation they would therefore be epicentrals, and their origin on the centrum or parapophysis (rather than on the rib) would again be autapomorphic. Among beryciforms, *Anomalops,* berycids, and holocentrids have true epineurals that originate on the rib anteriorly, rather than on the neural arch. G & B interpreted this as autapomorphic in holocentrids (they did not study anom-

alopids or berycids). There are other reasons (unrelated to the intermusculars) for placing *Polymixia* basal to other acanthomorphs, for placing stephanoberyciforms and beryciforms basal at least to all percomorphs (e.g., Stiassny, 1986; Stiassny and Moore, 1992; J & P), and for placing lampridiforms as the most basal acanthomorphs (J & P). Finally, we have now found (fig. 6) that the proximal part of the first epineural of *Velifer* lies in the horizontal septum (because the epicentral originates on it); G & B will presumably also interpret this as autapomorphic.

Reviewing the intermuscular bones of these lower acanthomorphs, we must question an interpretation that requires independent or autapomorphic modification in each of four groups, with origin of the bones ventrally displaced in *Velifer* and *Polymixia,* further ventrally displaced in beryciforms, but dorsally displaced in stephanoberyciforms. In other words, *Velifer* has part of the first intermuscular bone in the horizontal septum; *Polymixia* has the first and part of the second bone in that septum; holocentrids have the first two and parts of succeeding bones in that septum; and stephanoberyciforms have all the bones in the septum. The natural or parsimonious interpretation of these facts is that we are dealing not with four separate characters but with one transformation series.

The other feature of the intermusculars in which beryciforms and stephanoberyciforms differ from *Polymixia* is that they have two (or more) anterior intermusculars in the horizontal septum, rather than just that of V1. G & B agreed, interpreting the bone on V2 in holocentrids as an epicentral. Stated as a character, their interpretation becomes: *Second epineural reduced from a conspicuous bone to a diffuse array of collagen fibers and displaced dorsally, from base of neural arch to a broad area along the arch extending from a point above the dorsal margin of the centrum to near the base of the neural spine; second epicentral ossified and displaced dorsally from centrum to base of neural arch.* Taken with the similar convolutions necessary to explain the condition in *Polymixia,* this seems at the least improbable, if not a *reductio ad absurdum.*

G & B argued that their interpretation (acanthomorph intermuscular bones are epi-

centrals) explains three sets of data that conflict with ours (the bones are epineurals).

1. *All the intermusculars of paracanthopterygians, stephanoberyciforms and zeiforms are in the horizontal septum.* With the scheme of relationships in J & P this requires three independent acquisitions of that condition, because beryciforms (with some bones in the epineural position) are placed above those groups. G & B stated that with their interpretation the condition in paracanthopterygians, etc. "is the plesiomorphic retention of an epicentral bony series." But for what taxon is that the plesiomorphic condition? There are no epicentral bones in myctophiforms, the immediate outgroup of acanthomorphs. The second outgroup is aulopiforms, where epicentrals are ossified only in *Parasudis, Omosudis,* and *Alepisaurus,* clearly a derived condition (Baldwin and Johnson, 1996). In the third outgroup, stomiiforms, epicentral bones do not occur. G & B wrote "A series of epicentral bones may turn out to be a synapomorphy for their [J & P' S] Holacanthopterygii" (acanthomorphs less lampridiforms and polymixiiforms). This adds nothing. With either their interpretation or ours, to have all intermuscular bones in the horizontal septum is a derived condition somewhere within acanthomorphs.

2. *In percomorphs and zeiforms the most anterior POTs insert on intermuscular bones.* Our interpretation entails explaining this as a new, secondary association with ventrally displaced epineurals. G & B's interpretation makes the percomorph condition "retention of the plesiomorphic association" between epicentrals (as ligament) and POTS. In acanthomorph outgroups such as myctophids and stomiiforms, POTs extend forward to the most anterior vertebrae. For example, in the myctophid *Notoscopelus resplendens* (AMNH 25928SW, SL 55 mm) POTs inserting on the epicentral ligament of V1 originate on V3 and V4. In the stomiiform *Diplophos taenia* (USNM 206614, SL ca. 255 mm) POTs also originate on V3 and V4. We (P & J: 40) found that lampridiforms and *Polymixia* "are unique among acanthomorphs in having POTs that originate on abdominal vertebrae and insert on anterior epicentral ligaments (the first POT originates on V9 in *Polymixia* and *Velifer,* and inserts on the epi-

central of V5 in *Polymixia* and of V3 in *Velifer*)." If a full series of POTs is indeed the primitive neoteleost (or teleost) condition, basal acanthomorphs are modified in having reduced or lost anterior POTs.[3] Among paracanthopterygians, *Aphredoderus* has the most anterior POT running from V12 to myoseptum 9. In stephanoberyciforms, where POTs are present only in melamphaids, the foremost originates on or behind V10 (P & J, p. 40, reported V9 in *Poromitra*; we rechecked the specimen in alcohol and now place it on V10). In beryciforms the foremost POTs originate at V11 (*Anomalops*) or more posteriorly (V12 in *Hoplostethus,* V13 in holocentrids and *Photoblepharon*). Percopsiforms, stephanoberyciforms, and beryciforms therefore confirm that lower acanthomorphs have lost or reduced anterior POTs, and none of them has POTs extending so far forward as in *Polymixia* or *Velifer.* Given these observations, we dispute G & B's opinion that the anterior POTs of percomorphs retain "the plesiomorphic association" with epicentrals. In percomorphs so far sampled (P & J, unless another source is given), origin of the foremost POT ranges from about V15 in some long-bodied scombrids (Westneat et al., 1993: table 2), through V9–10 (e.g., *Centropomus, Serranus*). V7–8 (e.g., *Antigonia, Drepane, Lates, Sphyraena*; *Scomber*; Westneat et al., 1993: table 2), V5–6 (e.g., *Caranx, Mulloidichthys*), up to V3 (*Siganus*).

3. *"The concept of "neoneurals" in some percomorphs is superfluous because the "neoneurals" are true epineurals"* (G & B: p. 24). We find it remarkable that G & B do not appreciate the clear and consistent differences in structure distinguishing the "true" (undisputed) epineural ligaments that

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[3] G & B labeled POTs crossing the intermuscular bone of Vl in *Hoplostethus* (fig. 4B) and that of V2 in *Lates* (fig. 6F). In *Hoplostethus* this is part of a sheet of connective tissue (like that described on p. 9 in *Holocentrus ascensionis*) that originates on the heads of the second and third ribs and inserts on the first and second intermuscular bones. In our opinion, the first true POT in our *Hoplostethus* originates on the hemal spine of V12. In *Lates,* G & B's POT is part of a band of connective tissue that originates on the underside of the rib of V4, passes above the intermuscular and rib of V3, and inserts on the intermusculars of Vl and V2. It is not a POT.

they illustrate in *Polymixia* (fig. 2A), *Velifer* (fig. 3A), or *Hoplostethus* (fig. 4A) from the (in our view) "false epineurals" that they illustrated in anterior myosepta of those fishes (figs. 2B, 3C, D, 4B–D). The same clear differences distinguish the "neoneurals" that G & B illustrated in *Kuhlia,* carangids, and *Sphyraena* (figs. 9, 10) from the (in our view) "false epineurals" that they illustrated in paracanthopterygians, atherinomorphs, and lower percoids (figs. 6–8).

We still assert that true epineurals (above the horizontal septum) do not exist in percomorphs, and that the concept of neoneurals is valid and necessary. Lending further credence to this assertion, we believe, is the fact that the anteriormost neoneurals insert higher up the neural arch (at or near the base of the neural spine). The primitive and widespread insertion point of the anteriormost epineurals in teleosts is at the base of the neural arch (often in a modified articular depression or socket), near its junction with the centrum, the same position occupied by the first two intermuscular bones in percomorphs and other acanthomorphs. The position of neoneurals suggests the possibility that they may have consolidated within G & B's arrays of collagen fibers, but their absence in nonpercomorph acanthomorphs and their limited distribution among unrelated percomorph families indicate that they have arisen independently several times.

CONCLUSIONS

It is unfortunate that the differences between our interpretation (acanthomorph intermuscular bones are epineurals) and G & B's (they are epicentrals) turn out to depend, in part, on definition, or on the question "what is a ligament?" Our technique for studying the intermuscular system may have been primitive, but we were anxious not to over interpret. G & B have a superb technique for visualizing collagen in myosepta, but, as we have shown, the arrays of collagen fibers they interpret as representing the epineural series in most acanthomorphs are visible without dissection and polarization of myosepta and occur in *Polymixia* above an undoubted epineural bone. Nonetheless, they have forced us to reexamine many speci-

mens, and to acknowledge mistakes such as overlooking some anterior epicentral ligaments in holocentrids and anomalopids, mistaking epicentral ligaments for epineurals in *Hoplostethus* and so missing the epicentrals, missing the insertion on the epineural bone of epicentral 1 in *Velifer* and epicentral 2 in *Polymixia* (so failing to appreciate that these bones enter the horizontal septum), and missing the posterior epicentrals and POTs in *Aphredoderus* and the neoneural series in *Sphyraena*. But we find our major conclusion, that the intermusculars of acanthomorphs are descended epineurals, not only unshaken but reinforced. We have good evidence of mobility of an intermuscular series in the epipleurals of aulopiforms, which have moved up into the horizontal septum. We have evidence that anterior epineurals have moved down and entered the horizontal septum in *Polymixia*; in *Velifer*; and in anomalopid, berycid, and holocentrid beryciforms. We have shown why we consider the structures G & B call anterior epineural tendons [ligaments] in *Polymixia* and beryciforms to be wrongly identified. In lower acanthomorphs (paracanthopterygians, atherinomorphs, lower percoids) their "epineurals" are, without exception, diffuse arrays of collagen, as are the misidentified structures in *Polymixia* and beryciforms. Finally, we conclude that their interpretation of the first intermuscular in *Polymixia* and the first two in beryciforms as epicentrals would require unacceptable or unparsimonious convolutions of character transformation when considered in a phylogenetic context.

very special friendship. We probably spent the better part of one of those seven years together in London or Washington, where the work and play often ran seamlessly together, and we spoke often by phone when apart. Through all of it we laughed long, and hard, and often, and a day rarely passes that I don't feel Colin's absence. Of the several projects we worked on together, our two-plus year journey through the largely unexplored world of teleost intermusculars was perhaps the highlight, with each additional specimen offering the potential of new challenges, discoveries, and hypotheses of homologies and relationships. Although we never spoke of it, I think we both welcomed the opportunity the G & B paper provided for us to revisit some of our old friends, *Polymixia* et al.

The manuscript was completed, submitted, and revised after Colin's death, and any shortcomings in the way the reviewers' comments were or were not dealt with are mine alone. As official reviewers, I thank Dick Zusi and Mark Westneat. Westneat was responsible for G & B's decision to use the term tendon rather than ligament for unossified intermusculars, and, of course, he argued this point extensively in his review of this paper. The discussion of our decision to retain the term ligament is modified somewhat from the original version, but I am sure he will find it no more convincing. Sven Gemballa and Ralf Britz read and commented extensively on the manuscript; however, as with the manuscript of their 1998 paper, we agreed in advance that our differences were too great to be resolved in review. Nonetheless, I am grateful for their careful review and commentary, some of which led me to reexamine specimens and modify bits of text to clarify and hopefully better explain specific points, details of descriptions, and certain aspects of our argumentation. Still, the majority of their critique must go unanswered here, for to attempt to do so would require me to present each of their points and my response.

I am particularly indebted to Shirleen Smith for critical review and discussion of the manuscript, for assistance with additional observations during its revision, and perhaps most of all for caring enough about the sub-

ject to have read carefully J & P, G & B, and this manuscript, all on her own time.

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Figures, pages 20–24

1. *Polymixia lowei* Gunther, c & s specimen.

2. *Polymixia lowei* Gunther, c & s specimen. Myosepta removed and photographed in polarized light in ethanol.

3. *Coccorella atlantica* (Parr), first seven vertebrate, left side.

4. *Polymixia lowei* Gunther, c & s specimen in ethanol.

5. *Polymixia lowei* Gunther, c & s specimen in ethanol.

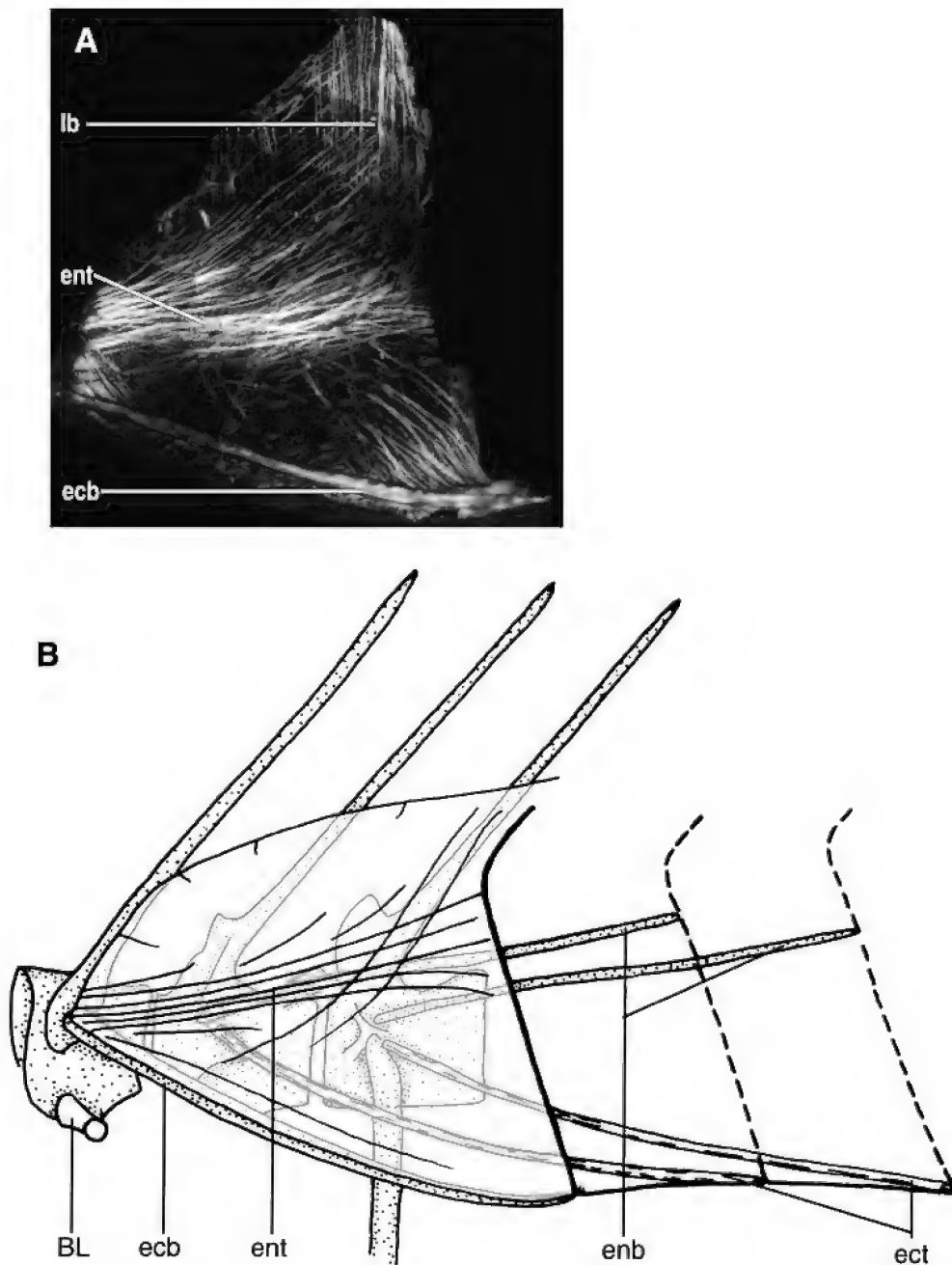6. *Velifer hypselopterus* Bleeker, c & s specimen in ethanol.

Fig. 1. *Polymixia lowei* Gunther, c & s specimen. **A.** Myoseptum 1 removed and photographed in polarized light in ethanol. **B.** Spatial relationship of epaxial myoseptum 1 and first three vertebrae and intermuscular elements. These are respectively figs. 2A and C of Gemballa and Britz (1998) with original labels (see Abbreviations under Terminology). Note different insertion area of ent in A (photograph) and B (drawing).
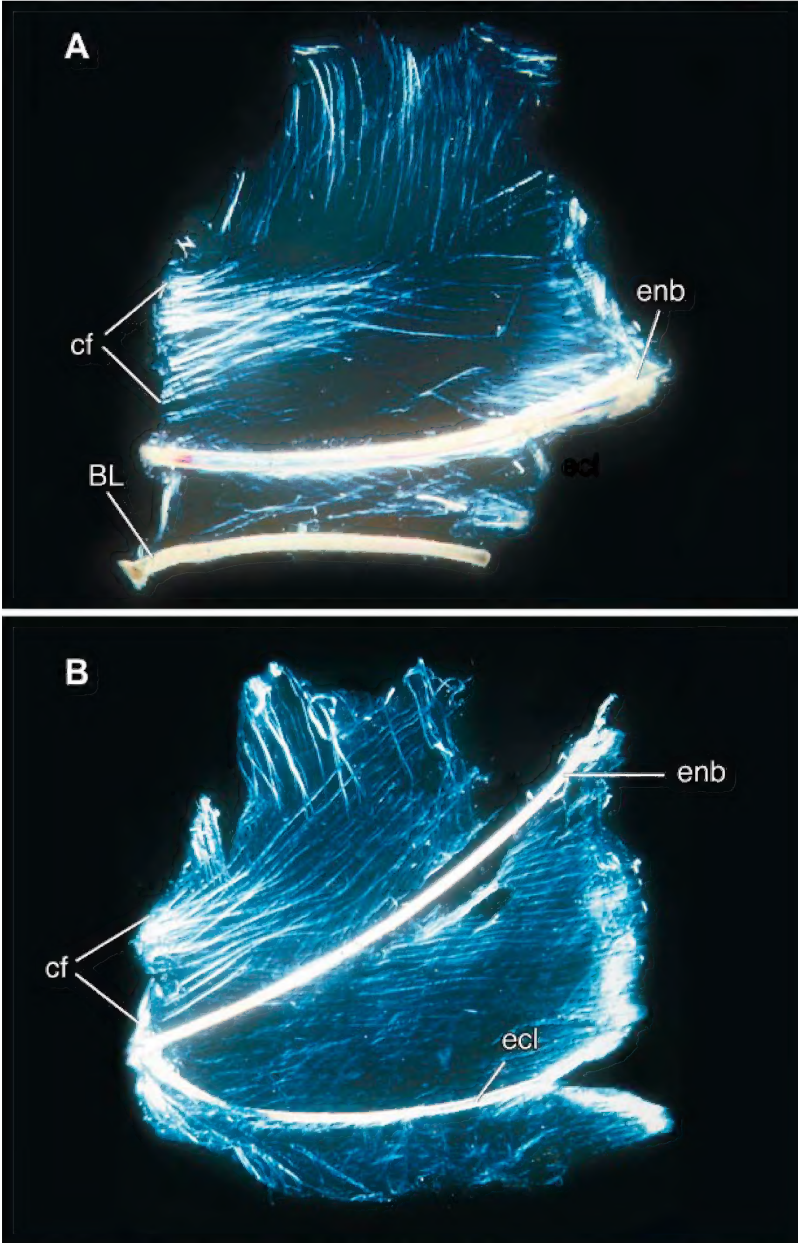
Fig. 2.   *Polymixia lowei* Gunther, USNM 185284, SL 75 mm, c & s specimen. Myosepta removed and photographed in polarized light in ethanol. **A.** Myoseptum 1 showing Baudelot's ligament (BL), the large intermuscular bone (enb), and above it the array of collagen fibers (cf) that G & B call the epineural ligament [tendon]. **B.** Myoseptum 2 showing the epineural bone (enb) with the epicentral ligament (ecl) originating on its base, and above it an array of collagen fibers (cf) like that in A.
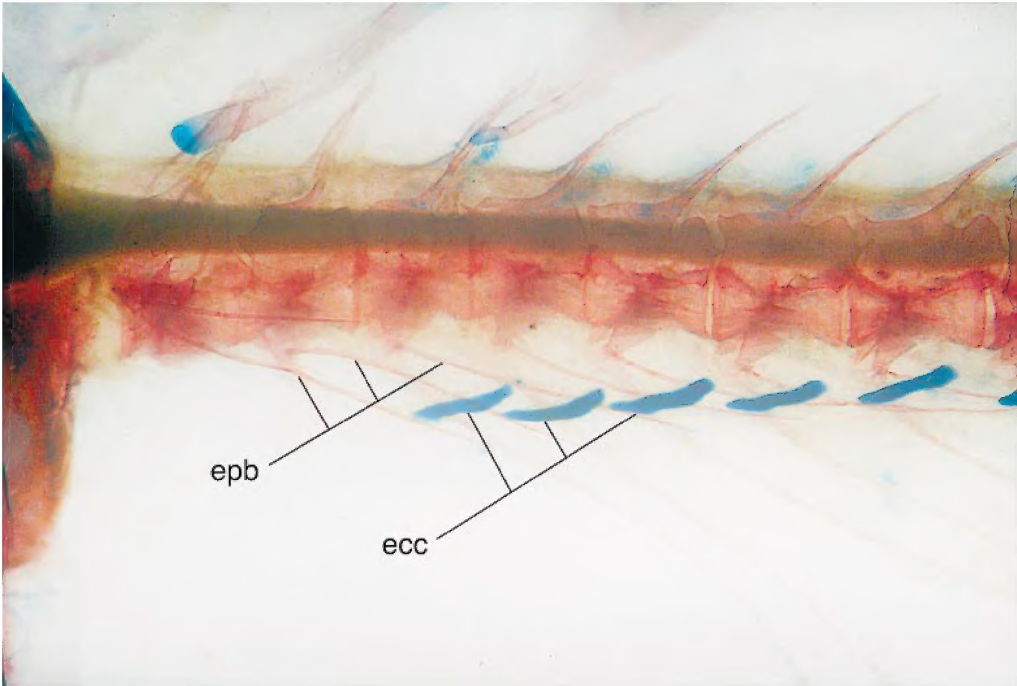
Fig. 3. *Coccorella atlantica* (Parr), USNM 235189, SL 60 mm, first seven vertebrae, left side. Epipleural bones (epb) of V1–5 have alcian-stained cartilaginous epicentrals (ecc) attached near their tips.
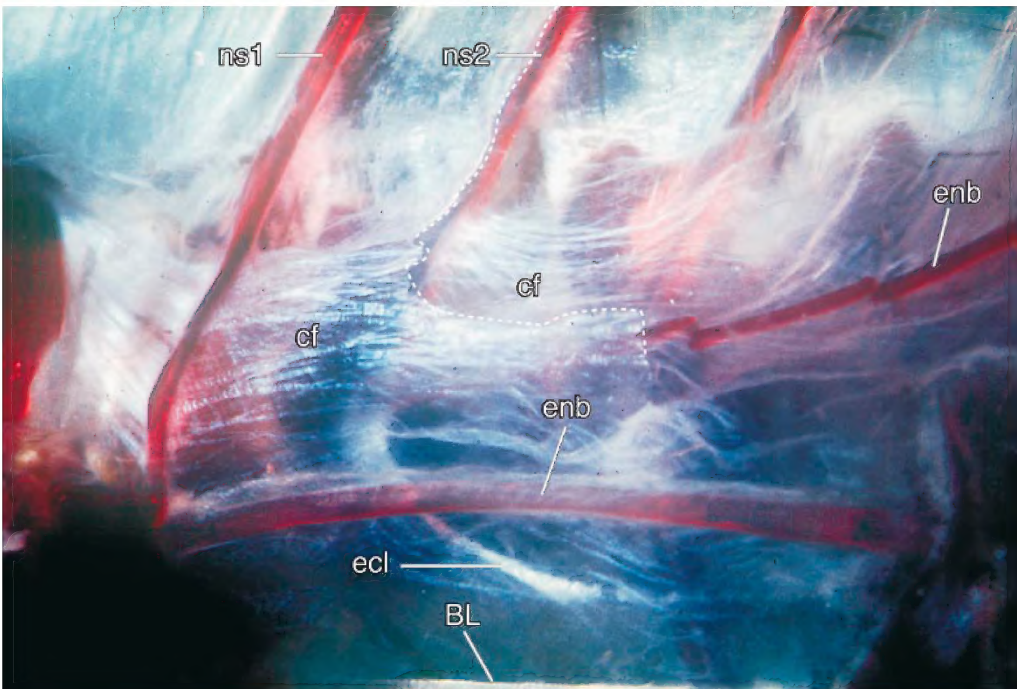

Fig. 4. *Polymixia lowei* Gunther, USNM 159300, SL 94 mm, c & s specimen in ethanol. The posterodorsal quadrant and entire posterior margin of myoseptum 1 have been cut away (dotted line) to expose the dorsal half of myoseptum 2 and the second neural spine (ns2). Note the origin of the downturned first epineural bone (enb) at the base of the neural arch and above it the array of collagen fibers (cf) inserting broadly along the dorsal extent of the neural arch to a point below the base of the neural spine (ns1). Through the window in the first myoseptum an array of collagen fibers (cf), identical to that of the first, is seen above the upturned second epineural bone (enb), which is broken. The epicentral ligament (ecl) of V2 can be seen through the ventral portion of myoseptum 1.
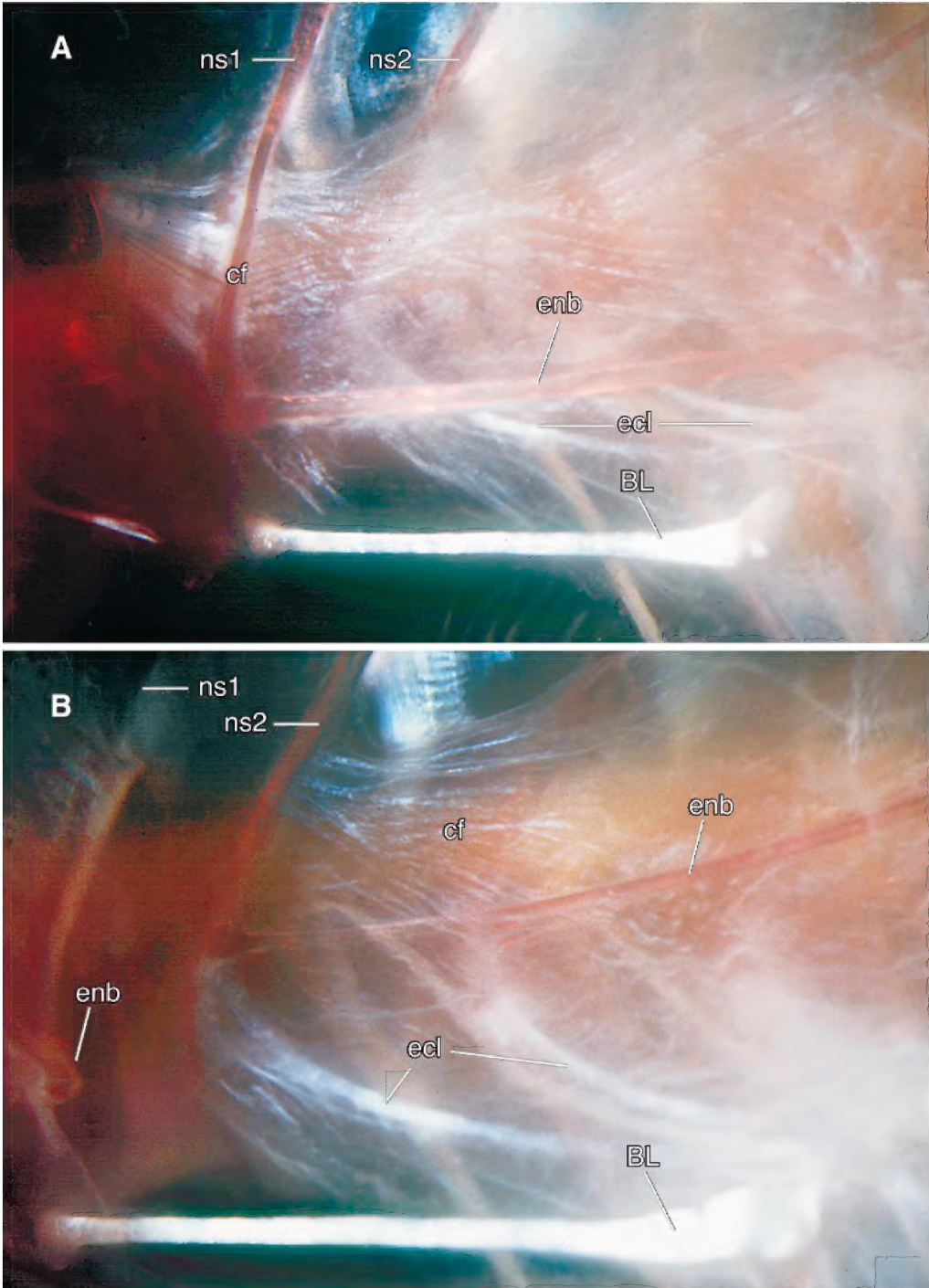
Fig. 5. *Polymixia lowei* Gunther, USNM 185284, SL 75 mm, c & s specimen in ethanol. **A.** Myoseptum 1, with Baudelot's ligament (BL) ventrally; above BL the intermuscular bone (enb) originates in a socket on the base of the neural arch, and above that an array of collagen fibers (cf) originates along the dorsal extent of the neural arch, between the dorsal margin of the centrum and the base of the neural spine (ns1). The distal part of the epicentral ligaments (ecl) of V2 and V3 can be seen through myoseptum 1. **B.** Myoseptum 2, after reflexion of myoseptum 1 (Baudelot's ligament [BL] remains as a landmark, and the base of the first intermuscular bone [enb] can be seen). The epicentral ligament (ecl) of V2 originates at the base of the intermuscular bone above it (enb), and above that an array of collagen fibers (cf), like that of the first, originates along the dorsal extent of the arch to just below the neural spine (ns2). The epicentral ligament (ecl) of V3 can be seen through myoseptum 2.
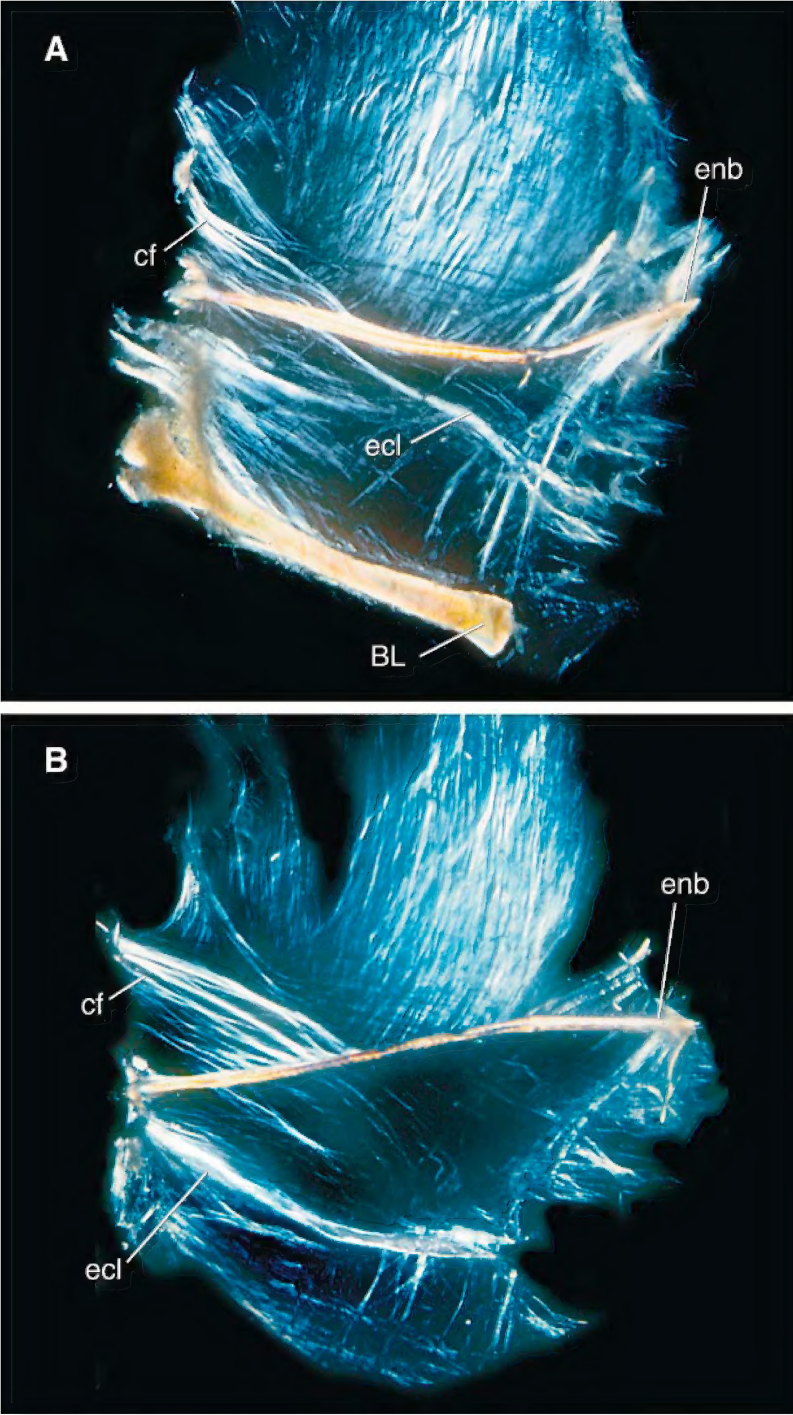
Fig. 6. *Velifer hypselopterus* Bleeker, AMS I 21848020, SL 95 mm, c & s specimen. Myosepta removed and photographed in polarized light in ethanol. **A.** Myoseptum 1 showing Baudelot's ligament (BL), a slender epicentral ligament (ecl) originating on the epineural bone (enb), and above the bone an array of collagen fibers (cf) that pass from the upper portion of the neural arch to the epineural. **B.** Myoseptum 2 showing the slender epicentral ligament (ecl), the epineural bone (enb), and above it an array of collagen fibers (cf) that insert on the epineural (enb), like those in myoseptum 1.